THE INTRODUCTION OF SIPHONINUS PHILLYREAE (HALIDAY) (HOMOPTERA: ALEYRODIDAE) INTO NORTH AMERICA: NICHE COMPETITION, EVOLUTION OF HOST PLANT ACCEPTANCE, AND A PREDICTION OF ITS POTENTIAL RANGE IN THE NEARCTIC

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Abstract.—Siphoninus phillyreae (Haliday), the ash whitefly, was initially collected in North America in Los Angeles, California, August 1988 and underwent a vast population explosion shortly afterwards. We document the current status of its expanding distribution in North America and note over 25 host plant species/varieties and five plant families that are used by this whitefly in California but unreported as hosts in its native Palaearctic range. We predict a potential ultimate range in the Nearctic for the whitefly, based upon isotherm data with reference to its Old World distribution. We list the diagnostic features of the species, and comment on the taxonomic status of *S. phillyreae*, noting that pupae from California seem closer in appearance to material from Egypt than from southern Europe. We suggest that acceptance of new host plants in California may be a mutation driven phenomenon with the increased host acceptance mutations due to its extreme and unchecked population size. We comment upon the potential host plant niches that this whitefly will occupy in the Nearctic, and the taxa that could be its most serious ecological competitors in these niches.

Key Words.-Insecta, Aleyrodidae, Siphoninus phillyreae, ash whitefly, Nearctic distribution, host plant evolution, niche competition

On 18 Aug 1988, *Siphoninus phillyreae* (Haliday), the ash whitefly, was collected for the first time in North America by R. Orsburn in Los Angeles, California. This species' previous distribution was palaearctic, from Ireland, Morocco and Cameroun in the west to India in the east. Shortly after its collection, an extraordinary population explosion of *S. phillyreae* occurred throughout the Los Angeles basin which was attributed to a lack of natural enemies. Populations grew rapidly with the flying adults described as appearing similar to a light snow flurry. Within a year the species distribution within California (Fig. 1) had spread along the southern California coast from Santa Barbara to San Diego, and ranged inland to Riverside (Riverside Co.), Victorville (San Bernardino Co.) and Lancaster (Los Angeles Co.) in the desert; by December 1989 it had expanded through California's central valley to Sacramento, and to San Jose in the San Francisco Bay Area, probably through the movements of infested plant material. In December 1989, *S. phillyreae* was found infesting nursery stock arriving in Los Angeles from Phoenix, Arizona; the whitefly had been found in Phoenix two months before.

The severe infestation found in the Los Angeles basin has caused honeydew and sooty mold problems, as is common with other whiteflies but seldom noticed



Figure 1. Distribution of Siphoninus phillyreae in California, as of December 1989.

because of their smaller populations. The whitefly is not dependent upon fresh, flush growth on its hosts as are several other aleyrodids (e.g., *Parabemisia myricae* [Kuwana], Walker & Aitken 1985) which have been recently introduced into California. Therefore, the entire shrub or tree canopy is subject to infestation during the season. Locally occurring aleyrodid natural enemies have not been found associated with the *S. phillyreae* populations. Although this whitefly has been reported to have two to three generations per year in Egypt (Priesner & Hosny 1932), it is thought to have considerably more in southern California with a potential generation time of 25 days (T. Bellows, personal communcation).

This explosive, invasive occurrence has revealed several interesting biological

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Figure 2. Pupae of *Siphoninus phillyreae* (after Priesner & Hosney 1932). Smaller pupae (described as *S. granati* by Priesner & Hosney) and larger pupae (figured as *S. phillyreae* by Priesner & Hosney). Note size related occurrence of siphon tubes on dorsomedial abdominal segments.

aspects about this whitefly which are atypical of most others that have become established in California. We comment upon some of these aspects and their evolutionary significance in the expanding allopatric distribution of this species.

TAXONOMY

Siphoninus phillyreae has a unique phena in its pupal stage. The living pupa is pale with a melanic stripe dorsomedially; its dorsum is covered with 'siphon tubes' that are somewhat similar in appearance to the siphunculi (cornicles) of aphids. Each siphon produces a droplet of wax that causes the entire structure to appear as a glassy club; there are 40–50 such clubs on each pupa. The pupae also have a dorsomedial series of tufts composed of white fibrous wax which form a dorsomedial line obscuring medially located siphon tubes.

Slide mounted pupae show these numerous siphon tubes and a dorsomedial melanic stripe that fades in the middle of the otherwise pale body (Fig. 2). Live adults are undistinguished, but slide mounted males have a single posteromedially directed tooth that is immediately anteriad of the terminal process (apical tooth) on each clasper (Fig. 3); this tooth is apparently homologous with the subapical tooth of the clasper (Gill in press) exhibited by other aleyrodids.

Mound & Halsey (1978) consider S. phillyreae to be a single, but variable species, noting that the number and placement of the dorsal siphons on its pupal



Figure 3. Male genitalia of Siphoninus phillyreae, dorsal view, anterior to top.

cases is variable and is related in part to the overall size of the pupal case (Goux 1949); see Fig. 2 for size-related variability in siphon numbers, where larger specimens reputedly show more siphons in dorsomedial series on the mesal portion of the abdominal dorsum. Mound & Halsey's (1978) assessment of *S. phillyreae* as a single (taxonomic) entity has considerable importance to its successful biological control because if a species-complex or series of biotypes were involved, it could complicate efforts to find compatible controlling agents.

Material in California thus far examined shows a characteristic heavy dorsomedial band of wax. However, CDFA efforts in August, 1989, to secure natural enemies in northern Italy and adjacent France found that *S. phillyreae* pupae in that area lack such a conspicuous wax band (L. Bezark, personal communication). The California material appears similar to Egyptian material of *S. granati* Priesner & Hosny (1932: plate 1) described from pomegranate. That species nomen, as well as *inaequalis* Gautier, *dubiosa* Haupt, *dubious* Heeger, *phylliceae* Bouché, *finitimus* Silvestri, and *multitubulatus* Goux, have been synonymized under *phillyreae* Haliday by Mound & Halsey (1978). It will be interesting to find out if imported and released biological control agents "recognize" such taxonomic treatment.

BIOLOGY

Potential Nearctic Range. – We suspect that S. phillyreae, if it is a single and uniform biological entity with respect to temperature tolerances, will continue to



Figure 4. Isotherm map of Europe for average daily temperature in January. Siphoninus phillyreae occurs throughout the area shown, north to approximately the -7° C (20° F) isotherm, except in southern Norway and Sweden.

expand its range well into temperate North America. This is because unlike many more tropical aleyrodids that have been introduced into California, such as *Aleurothrixus floccosus* (Maskell) or *Dialeurodes citrifolii* (Morgan) (Dowell & Gill 1989), *S. phillyreae* occurs well north into Europe in Germany, Poland and the western and southern U.S.S.R. Its Palaearctic distribution appears limited to south of isotherms for an average January daily temperature of between -7° C (20° F) and -1° C (30° F) (Fig. 4), although it has not been reported in southern Norway or Sweden (Huldén 1986) which also fall into this zone. If these same isotherms are also limiting in North America, *S. phillyreae* could potentially expand its range well into the Nearctic (Fig. 5) to southwestern British Columbia, western Montana, southern South Dakota, extreme southern Minnesota, and eastward across southern portions of Wisconsin, Michigan, and Ontario, to New England.

Host Associations. — This whitefly is polyphagous on relatively hard-leaved shrubs and small trees in the Palaearctic, where it shows host associations in the Oleaceae (Fraxinus, Olea, Phillyrea) and the Rosaceae (Crataegus, Cydonia, Mespilus, Prunus, Pyrus), but is also recorded from the Leguminosae (Afzelia), Punicaceae (Punica), Rhamnaceae (Rhamnus) (Mound & Halsey 1978) and Rutaceae (Citrus) (Khan et al. 1985). In California, S. phillyreae has been found on many hosts (Table 1) including over 25 species (and varieties) and five families not recorded in the Palaearctic. (This list has been updated while in press to reflect additional hosts reported by Bellows et al. [1990] and subsequent data, these have not [yet] been verified by CDFA.)

Although S. phillyreae has been found to use many new plants in California, it shows some differentiation in its acceptance of hosts. The preferred hosts in California have thus far been evergreen ash (*Fraxinus uhdei* [Wenzig] Lingelsheim) and evergreen (flowering) pear (*Pyrus kawakamii* Hayata), which seem particularly susceptible with large populations causing partial defoliation (Gill 1989). In con-



Figure 5. Isotherm map of North America for average daily temperature in January. As judged by its distribution in Europe with relation to climate, *Siphoninus phillyreae* should be able to tolerate those areas in North America north to the -7° C (20° F) or at least the -1° C (30° F) isotherm line.

trast, this whitefly seems to use *Rhaphiolepis* (K. Arakawa, personal communication) and *Citrus* mostly during winter months in southern California, when preferred deciduous hosts are barren.

Siphoninus phillyreae appears to survive the winter in all stages in southern California on some of its nondeciduous hosts (e.g., Citrus, Rhaphiolepis, Heteromeles). This facultative use of "overwintering" hosts in such climates has no doubt aided S. phillyreae in building up the dramatic numbers that are reported in the Los Angeles basin. By using evergreen overwintering hosts in California, populations of this whitefly need not crash in the fall, when their preferred deciduous hosts are unavailable. This permits a large number of surviving individuals in the spring to allow a greater population growth during the next season, as seen in the expression: population growth $= r_m N$, where r_m is the species' innate capacity for increase (Andrewartha & Birch 1954) and N is the surviving population in the spring. As S. phillyreae moves into more continental climates in the Nearctic, we expect that it will cease to have year-around breeding populations and that it will necessarily exhibit the distinct seasonality seen in northern Europe.

Evolution of Host Acceptance.—The prediction of ultimate range potential in the Nearctic assumes that compatible hosts are available and that the source population for the California introduction has an unrestricted genetic tolerance

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for cold with respect to the overall genome of S. phillyreae. Since "founder" populations are considered to classically show restricted genetic variance with respect to entire parental populations across their geographic ranges (Lewontin 1974), it is doubtful the last assumption is true. Alternatively, however, California populations of walnut husk fly, Rhagoletis completa Cresson, derived from introduced founders from parental populations in eastern North America, have been found (Berlocher 1984) to have developed both differing patterns of isozymic variation and greater isozymic variation around individual locii, than occurs in the populations in eastern North America. Hence, evolutionary mechanisms apparently exist in some cases to increase genetic variance and heterozygosity in populations derived from genetically restricted founder groups. Such newly discovered and poorly understood evolutionary mechanisms make potential and rapid evolutionary change under allopatric conditions over short time periods increasingly feasible and probable; this is because the genetic variance of daughter populations may be increased, allowing them to meet selection pressures of their new environment that their parental populations were not subjected to.

One potential result of such an evolutionary mechanism in the case of S. *phillyreae* might be the increase in acceptable host plants (both as numbers of species and particularly families) that we report as used in California in comparison to the Palaearctic. The increase in acceptable hosts is no doubt a result of either favorable allelic (re)combinations or mutations allowing exploitation of a new host. Such host plant utilization models based upon genetic variance and combinations have been proposed in tephretids previously (Bush 1969, 1975). Under these models, the genetic variance in some *Rhagoletis* species has been considered great enough to create discrete behavioral traits for host selection; because mating occurs on hosts this has led to differentiation of mating sites and therefore to potential sympatric speciation between individuals accepting different hosts. It is doubtful, however, that simply new allelic combinations alone (barring mutations) are responsible for the increased level of host acceptance seen in California for S. phillyreae, because surely such recombination would have occurred previously in the species' palaearctic range. Rather it is likely that mutations have caused the observed increase in host acceptance.

Ordinarily, mutations are usually estimated to occur at one mutation per 10^{-5} or 10⁻⁶ individuals in the natural environment for organisms in general (Mettler & Gregg 1969). This rate has been reported to be as high as more than 1 per 10^{-4} for some traits in *Drosophila* (Dobzhansky 1970). Clearly, at these higher rates (> 1 mutant individual per 10,000) the explosive population growth exhibited by S. phillyreae in California (or other new agricultural pests in new environments free of natural enemies) would provide adequate numbers from which new acceptable host plant mutants might occur. Normally, the number of mutations in populations shows a balance between those mutations imparting an increased selective advantage and those that are lethal or sublethal. When populations suddenly begin to grow rapidly, however, the ascendancy of advantageous genes do not necessarily have to occur at the expense of normally lethal genes; the latter would thus functionally be eliminated more slowly (Emlen 1973). This is because if lethal genes were initially in equilibrium in a population, any rapid population increase would lessen the selection pressures upon them (in terms of population rather than individual response), allowing their frequency to increase, and ulti-

Family	Species	Common name
Apocynaceae: ^{a,c}	Plumeria rubra L.ª,c	plumeria
Bignoniaceae: ^a	Catalpa sp. ^{a,b}	catalpa (hybrid)
Leguminosae:	Cercis occidentalis Torrey ^a	western redbud
	Cercis siliquastrum L. ^{a,c}	Judas tree
Lythracaceae: ^a	Lagerstroemia indica L.ª	crape myrtle
Magnoliaceae: ^a	Liriodendron tulipifera L.ª	tulip tree
	Magnolia koba stellata Maximowicz ^a	star magnolia
Oleaceae:	Fraxinus latifolia Bentham ^{a,c}	Oregon ash
	Fraxinus uhdei (Wenzig) Lingelsheim	Shamel ash
	<i>Fraxinus uhdei</i> (Wenzig) Lingelsheim 'Tomlinson' ^{a,c}	Tomlinson ash
	Fraxinus velutina Torrey 'Modesto'a,c	Modesto ash
	Fraxinus velutina var. glabra Rehder ^a	Arizona ash
	Fraxinus velutina var. coriacea (Watson)	western (or leather-
		near) ash
	Dhillynog latifolia I	
	Philipfea lalifolia L.	philiprea
	Syringa × hyacininijolia (Hort. Lemoine) Kender ^a	excel filac (nybrid)
	Syringa laciniata Miller ^{a,c}	cut-leaf lilac
D '	Syringa vulgaris L.ª	lilac (or common lilac)
Punicaceae:	Punica granetum L.	pomegranate
Kosaceae:	Amelanchier sp. ^{4,0}	serviceberry
	Chaenomeles speciosa Nakai ^a	flowering quince
	Eriobotrya deflexa (Hemsley) Nakai ^a	golden loquat
	Eriobotrya japonica (Thunberg) Lindley ^{a,c}	loquat
	Heteromeles arbutifolia (Aiton) M. Roemer ^a	toyon
	Malus floribunda Siebold ^a	Japanese flowering crabapple
	Malus fusea (Rafinesque) C. K. Schneid ^a	Oregon crabapple
	Malus scheidecker Zabel ^a	Scheider crabapple
	Malus pumila P. Miller ^e	apple
	Malus sp. 'Hopa'a,c	crabapple
	Malus sp. 'Red Jade'a,c	crabapple
	Prunus armeniaca L.ª	apricot
	Prunus × blireiana Andre ^a	blue plum (hybrid)
	Prunus salicina Lindley 'Santa Rosa'a	Santa Rosa plum
	Prunus virginiana var. melanocarpa (A. Nelson)	chokecherry
	$Pvracantha sn^{a}$	firethorn
	Purus callervana Decaisne	ornamental pear
	Purus communis I	pear
	Pyrus kawakamii Hayata ^a	evergreen near
	Purus nurifolia Nakai	Iapapese sand pear
	Rhanhiolonis indica Lindleva	Japanese sano pear Indian hawthorn
Rubiacaaa.a	Conhalanthus occidentalis vor californiaus	huttonhush
Rublaceae."	Bentham ^a	buttonbush
Rutaceae:	Citrus aurantifolia Swingle ^a	lime
	Citrus limon (L.) Burman f. 'Meyer'a	Meyer lemon
	Citrus reticulata Blanco	tangerine
	Citrus sinensis Osbeck 'Valencia'a,f	Valencia orange
	Fortunella sp. ^{a,c}	kumquat

Table 1. Hosts recorded for Siphoninus phillyreae in California from which adults have emerged.

^a Host associations recorded from California only.
^b Hybrid species reported as "× Chiopa."

mately allowing the incorporation of these normally lethal genetic factors into the genetic variance in ways which may occasionally prove to be beneficial innovations (Emlen 1973). (For instance, a mutation allowing use of a new host plant might be functionally lethal or sublethal to a species with a requirement for sexual [recombinant] reproduction, if a mutated female on the new host could not find mates which occur on the normal host[s].) The result is that more rapidly fluctuating populations generally display a greater increase in changes for selected traits than do stable populations (Ford 1971).

An alternative explanation for *S. phillyreae's* increase in host acceptance in California over that of the Palaearctic is that previous host reporting in the Old World was inadequate. This is unlikely, however, because the whitefly is a serious agricultural pest and has been examined by many workers (for a bibliography see Mound & Halsey 1978). Furthermore, it is not uncommon for other exotic whiteflies to show similar increases in host acceptance during the phase of unrestrained population growth that initially follows their introduction into a new environment (RVD, unpublished data). Models currently under development treat expansion of host plant acceptance in species invading new environments, with particular reference to agricultural pests (RVD, unpublished data).

Niche Competition. — In addition to lacking natural enemies, S. phillyreae is almost devoid of competitors in California (especially rosaceous plants). Species of Citrus are the only hosts of S. phillyreae, either previously reported or new (Table 1), that are attacked regularly by a complement of whiteflies in California (RJG, unpublished data). However, S. phillyreae uses Citrus primarily as an overwintering host in California. Interestingly, Citrus are the chief evergreen hosts of S. phillyreae in California with a substantial but facultative fauna of polyphagous aphids (Kono & Papp 1977).

Because many genera of aphids in a "Rosaceous series" within the Aphidinae have evolved using plants in the Rosaceae as a primary (overwintering) host (Hille Ris Lambers 1950, 1979; Blackman & Eastop 1984; Dixon 1987), aphids are perhaps the most likely Homoptera to seriously compete with *S. phillyreae* for the niche of feeding on deciduous leaves in the Rosaceae. Several aphid groups have radiated using the Rosaceae in this way (e.g., the Rhopalosiphini: *Hyalopterous, Hysteroneura, Melanaphis, Rhopalosiphum, Schizaphis*; and the Macrosiphini: *Anuraphis* through *Macrosiphum*; among others). These holocyclic aphids have evolved using a life cycle employing woody plants in the Rosaceae as overwintering hosts, upon which to deposit their eggs in the fall. They move from the Rosaceae after completing a few generations in the early spring, having taken advantage of the high amino-nitrogen content of the rapidly growing leaves during spring foliation (Dixon 1970, 1973, 1977). When the amino-nitrogen content of

^c Host added while in press to reflect an update after Bellows et al. (1990) and subsequent data. Identification not (yet) verified by CDFA.

^d Reported as *Amelanchier* "*dentiolata*" for which we can find no species reference in taxonomic works.

^e Reported as M. domestica, which is crabapple, but assumed here to be common apple due to the common name association of "apple" on the record (Bellows et al. 1990 lists this record as M. domestica).

^f Also recorded from navel oranges but without reference to a particular cultivated variety.

the maturing leaves on these woody rosaceous hosts drop, the aphids customarily emigrate to rapidly growing herbaceous plants during the summer, again because of the higher available amino-nitrogen during their summer growth season. In the fall, as the herbaceous plants decline, the summer populations of these holocyclic aphids immigrate back to their woody Rosaceae overwintering hosts, where the amino-nitrogen content of the senescent leaves increases as leaf proteins are broken down. An advantage of this heteroecious life mode for holocyclic aphids is that favorable amino-nitrogen sources can be tracked throughout the year, and that foliating woody hosts in the early spring provide a dependable nutrient source when the aphid's eggs hatch into poorly mobile first instar nymphs that require immediate and adjacent high-quality food.

An ecological strategy of heteroecy and holocycly for aphidine aphids has many exceptions, however. In warmer areas, such as California, many species of these otherwise heteroecious aphid genera have adapted an anholocyclic strategy and have become secondarily monoecious by remaining continuously parthenogenetic on the ever-present growth of herbaceous plants. Many aphids considered serious agricultural pests (e.g., Myzus persicae [Sulzer], Aphis gossypii Glover) are polyphagous and anholocyclic, taking advantage of whatever happens to be the best amino-nitrogen source at the moment. Other entire aphid genera in rosaceous evolutionary series have similarly adopted a secondarily monoecious strategy (e.g., Sitobion) and have moved permanently to herbaceous plants in noncontinental climate areas. In contrast, some holocyclic species of Aphidinae (e.g., Aphis pomi DeGeer) remain on their rosaceous hosts continuously. The abandoning of midsummer teneral leaves with lower amino-nitrogen contents is not trivial for aphids; some more primitive aphid groups that are monoeciously restricted to trees (e.g., drepanosiphines and some phyllaphidines) must cope with lower available nutrients during the summer by ceasing reproduction and estivating as nymphs until amino-nitrogen raises in the fall (Hille Ris Lambers 1966).

Nonaphid homopterans do not have such a strong and definite evolutionary link with the Rosaceae, and either do not regularly feed on the deciduous leaves of plants in the Rosaceae (e.g., Coccoidea, Aleyrodoidea), or appear to occupy that niche as a relatively modern and derived "host capture" (e.g., several typhlocybine leafhopper genera, *Cacopsylla* [Psyllidae] on *Pyrus, Parthenolecanium corni* [Bouché] [Coccidae] nymphs on leaves during the summer).

Among S. phillyreae's favored nonrosaceous and deciduous hosts, aphids again appear as potential competitors. For example, *Fraxinus* is commonly used by *Prociphilus americanus* (Walker) and *P. fraxinifolii* (Riley) as an overwintering host (Kono & Papp 1977); these aphids, however, are also holocyclic, using conifers (Smith 1969) as secondary hosts during the summer.

In contrast to aphids, S. phillyreae prefers mature (teneral) foliage and is present during the hot summer months on its deciduous hosts; this largely eliminates or minimizes the synchronic use of these plants by this whitefly and aphids. Thus, S. phillyreae appears to occupy a reasonably distinct and somewhat unoccupied or less competitive niche that involves the summer use of teneral leaves among plants in the Rosaceae and Fraxinus. With no natural enemies or serious competitors, the population of S. phillyreae has rapidly increased in California and the whitefly has expanded its host plant range onto previously unused plants.

Economic Potential as a Pest. - Lacking competitors S. phillyreae will become

a major summer feeding pest of stone and pome fruits and numerous ornamental trees in California and elsewhere in North America. As such it could seriously disrupt existing management programs on these plants as has occurred with other whiteflies on *Citrus* (Dowell in press). In addition, management sprays for other pests such as codling moth, *Cydia pomonella* (L.) and oriental fruit moth, *Grapholitha molesta* (Busck) could interfere with biological control efforts (Dowell in press) aimed at *S. phillyreae*.

The apparent requirement for an overwintering host in California will limit the impact of *S. phillyreae* to those deciduous hosts near stands of overwintering hosts. Such situations for *S. phillyreae* commonly exist throughout California in urban and agricultural settings with *Citrus, Rhaphiolepis* and *Heteromeles*; particularly the latter in foothill areas near orchards. A similar situation exists for *Trialeurodes vittata* (Quaintance) which is a pest in grape vineyards near stands of its overwintering host, *Rhamnus californica* Eschecholtz (Joos 1981).

The extent of genetic variance in Californian S. phillyreae and its ultimate expression and consequences remain unknown. We suggest that studies of isozymic variation in the introduced Californian population, as it expands, in comparison with similar studies of variation for the Palaearctic may be of significant importance to both pragmatic economic estimates for the species as well as to an increased knowledge of evolutionary parameters and mechanisms in general. We suspect that eventually when successful natural enemies are introduced to control S. phillyreae populations in California, the variety of host plants which it occurs on will collapse to only those it does best on physiologically, ecologically and competitively. We also suspect, however, that this species will be a significant aleyrodid pest to some deciduous plants throughout its eventual Nearctic range.

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